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**FURTHER OBSERVATIONS ON THE FUNCTIONAL MORPHOLOGY OF THE
HEAD AND MOUTHPARTS OF DRAGONFLY LARVAE (ODONATA)**

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*Quaestiones Entomologicae
12: 89-114 1976*

*The structure and musculature of the head and mouthparts of last instar larvae of *Aeshna interrupta lineata* Walker and *Libellula quadrimaculata* L. are described. Particular attention is paid to the features related to protraction of the labium, including the T-shaped hypopharyngeal apodeme and the musculature in the elbow and at the base of the labium. Motion picture recordings of the strike using camera speeds of up to 200 frames per second have allowed a more detailed analysis of the strike than has previously been possible. The protraction of the labium is arbitrarily divided into five phases and an explanation for the characteristics of this sequence is offered. The primary force causing protraction of the labium is the hydraulic pressure developed by contraction of the lateral muscles of the thorax and abdomen. However the flexor muscles of the prementum are believed to be contracted during the early stages of pressure build-up, and their sudden release would then provide a mechanism whereby additional force is put into the strike. Such a proposal is supported by observations on the strike and also by recordings of pressure changes in the thorax made by Olesen (1972). The T-shaped apodeme provides support for the labial base, acts as the hinge for the postmentum, serves as the attachment point for important muscles, and through its elastic properties allows the postmentum to return after the strike.*

*Nous décrivons la structure et la musculature de la tête et des parties mandibulaires du dernier stade larvaire de *Aeshna interrupta lineata* Walker and *Libellula quadrimaculata* L. Nous avons payé une attention particulière aux caractéristiques liées à la protraction du labium, incluant les apodème hypopharyngéale en forme de T et à la musculature dans le coude et à la base du labium. Une film pris à l'aide d'une caméra enregistrant jusqu'à 200 images par seconde nous a permis d'analyser en plus grand détail le mouvement de l'attaque. Nous avons divisé la protraction du labium en cinq phases arbitraires, et nous offrons une explication pour les caractéristiques de cette séquence. La pression hydrolique développée lors de la contraction des muscles latéraux du thorax et de l'abdomen devient la force primaire causant la protraction du labium. Cependant nous croyons que les muscles fléchisseurs du prémentum sont contractés très tôt au début du développement de la pression, et que leur relâchement soudain créerait à ce moment un mécanisme par lequel une force additionnelle s'ajoute dans le mouvement d'attaque. Les observations sur les mouvement d'attaques et l'enregistrement du changement de pression dans le thorax par Olesen (1972) supportent une telle proposition. L'apodème en forme de T fournit le support nécessaire pour la base du labium, agit comme charnière du postmentum, sert comme point d'attachement pour d'importants muscles, et permet le retour du postmentum après l'attaque grâce à ses propriétés élastiques.*

INTRODUCTION

In recent years several papers have appeared on the predatory behavior of larval Odonata (e.g. Buchholtz, 1970; Richard, 1970; Caillère, 1972, 1973). The precise mechanism of the strike still remains unclear, however. This paper presents previously unpublished observations (Pritchard, 1963) on the morphology of the head and mouthparts of larval Anisoptera, some

new data on the strikes by *Aeshna canadensis* Walker and *Argia vivida* Hagen, and an hypothesis to explain labial protraction.

THE MORPHOLOGY OF THE HEAD AND MOUTHPARTS OF LARVAE OF ANISOPTERA

Snodgrass (1954), Asahina (1954), and Short (1955) have given descriptions of the structure and musculature of the head and mouthparts of larvae of *Anax junius* Drury, *Epiophlebia superstes* Selys, and *Aeshna cyanea* Müller respectively, but comparable descriptions for libellulid larvae are lacking.

There are two main types of head structure in larvae of Anisoptera; in the aeshnoid type (Petaluridae, Gomphidae, Aeshnidae) the head is prognathous and the labium is flat (Fig. 1), while in the libelluloid type (Cordulegasteridae, Synthemidae, Corduliidae, Macrodiplactidae, Libellulidae) the head is more nearly hypognathous and the labium is spoon-shaped (Fig. 2). In the following account, last instar larvae of *Aeshna interrupta lineata* Walker and *Libellula quadrimaculata* L. are taken as representative of these two types.

The nomenclature used here follows Snodgrass (1935) for the most part. The homologies of the distal lobes of the maxilla have been the subject of controversy in the past, but as Snodgrass (1954) and Short (1955) have pointed out, the arrangement of the muscles precludes the presence of a galea and points to the inner lobe being the lacinia and the outer lobe the palp. There has also been some confusion over the terminology of the parts of the labium, for some authors have used the terms "mentum" and "submentum" for the sclerites of the prelabium and postlabium respectively. Corbet (1953) drew attention to this and proposed the use of the terms "prementum" and "postmentum" in accordance with Snodgrass's (1935) definition. The terminology for the muscles of the labium follows Munscheid (1933).

Aeshna interrupta

Several features of the head capsule (Fig. 3 and 4) are associated with the structure of the labium and the method of prey capture. The head is flattened and prognathous so that the mouthparts project forwards in a position to receive prey that is brought back by the labium. The compound eyes are large and cover much of the front and sides of the head, especially in later instars, and consequently there is a reduction of the genae. Lew (1933) has described the development of the eyes during the larval stages of *Aeshna umbrosa* Walker, and morphology of the eyes in relation to prey capture was considered by Pritchard (1966).

The coronal sulcus (cs) is well defined and branches anteriorly into the postfrontal sulci (pfs) which run between the compound eyes (ce). Three areas of pigmentation (oc) on the vertex (vx) mark the positions of the ocelli. The antennae play little if any role in prey detection, at least in larger larvae (Pritchard 1965a). They have seven articles and are borne on raised areas bordering the frons (fr). Between these areas and the compound eyes are the dorsal tentorial maculae (td). The clypeus is large, convex and weakly divided into ante- and post-clypeus.

The posterior wall of the head capsule is concave and slopes in to the occipital foramen (for) on all sides. The postocciput (po) is a narrow sclerite around the foramen and the posterior tentorial pits are clearly visible in the bases of the postoccipital sutures (pos). There is no distinct division between the occiput (o) and the genae (gen), but the occipital sulci (os) are present from the level of the posterior tentorial pits to the posterior articulations of the mandibles, thus marking off the postgenae (pg). The hypostomal border of the head capsule and the postoccipital suture form strong ridges in the region of the posterior articulation of the mandible (pam), providing a rigid framework for the support of this area during feeding.

The tentorium (pat, aat) is *pi*-shaped with anterior, posterior and dorsal arms all well-developed

and forming a strong endoskeleton for the support of the head capsule and for the attachment of certain muscles. The attachments of the dorsal and posterior arms have already been mentioned; the anterior tentorial pits (ta) may be seen between the eyes and the bases of the mandibles.

The labrum of *Aeshna interrupta* (Fig. 5 and 6) is widest at its free anterior end and is three times as wide as long. The epistomal sulcus is well defined. Aborally the labrum is well sclerotized and the adoral side is membranous and bears gustatory sensilla (Pritchard, 1965b). There are three pairs of labral muscles. The labral compressors (cplr) are a median pair entirely within the labrum and inserted on its dorsal and ventral walls. The anterior labral muscles (mlra) insert medially at the labral base on the dorsal side and originate widely apart on the frons. The posterior labral muscles (mlrp) insert on the tormae at the proximal angles of the labrum on the ventral side and they originate with the anterior labral muscles on the frons.

The mandibles (Fig. 7 and 8) are stout, heavily sclerotized appendages. Four incisor teeth are placed in a single line (in) at the distal end and below these is a ridge (mo), usually called the molar ridge, with a tooth at each end. The molar ridge is, however, badly named since its function is slicing rather than grinding. The base of the mandible is triangular with anterior, posterior, and inner angles; the anterior and posterior angles articulate with the clypeus and the subgena respectively. There are four muscles, two dorsal and two ventral, which serve the mandible. The dorsal adductor (dad) is very large and originates over a wide area of the posterior wall of the head capsule; it inserts through a small apodeme at the inner angle of the mandibular base. The dorsal abductor (dab) is smaller; it originates on the head capsule below the adductor and inserts through an apodeme just in front of the posterior articulation of the mandible. The ventral muscles are small; one of them (vmh) originates on the base of the hypopharynx and is inserted inside the cavity of the mandible on the lateral wall, and the other (vmt) originates on the anterior arm of the tentorium and is inserted inside the cavity of the mandible on the posterior wall.

The maxilla (Figs. 9 and 10) has a one-segmented, flattened palp (mxp) and a broad lacinia (lc) that bears seven sharp teeth and many long, stiff setae. Each maxilla is served by seven muscles, two of which originate on the head capsule between the dorsal mandibular muscles, two originate on the body of the tentorium, and three originate within the stipes. Originating on the head capsule are the anterior rotator of the maxilla (rtmxa) which inserts at the base of the cardo, and the cranial flexor of the lacinia (flcc) which inserts close to the base of the lacinia. The adductor of the cardo (adcd) and the adductor of the stipes (adst) originate on the body of the tentorium. From the stipes (stp), the stipital flexor of the lacinia (flcs) inserts with the cranial flexor, the depressor of the palp (dpmp) inserts at the outer angle at the base of the palp, and the levator of the palp (lvmp) inserts on the inner angle of the palpal base. The latter two muscles are small and originate together at the distal end of the stipes.

In the labium (Fig. 11 and 12) the sclerites can be homologized, but some of the muscles cannot be correlated with those of a generalized insect labium. The postmentum (pom) of *Aeshna interrupta* is flat and elongated and the prementum (prm) is spatulate. The labial palps are pincer-like and two-segmented; the first segment forms the body of the palp and is projected distally as a blunt "end-hook" (eh), and the second segment is a sharp "movable-hook" (mh).

Two muscles are inserted at the base of each palp. The abductor of the palp (ablp) originates on the dorsal wall of the prementum and inserts through a small apodeme at the outer corner of the base of the palp. The adductor of the labial palp (addlp) is a larger muscle which originates on the ventral wall of the postmentum just proximal to the elbow and inserts at the inner corner of the palpal base.

There is a single pair of extensor muscles of the prementum (exprm), which originate on the tentorium and are inserted through long apodemes on lever-like extensions of the prementum past the hinge.

Three pairs of muscles appear to have flexor functions. The primary flexors of the prementum (1° fl) are large, originating on the T-shaped apodeme of the hypopharynx and inserting on the ventral wall of the prementum just distal to the elbow, and the secondary (2° fl) and tertiary (3° fl) flexors are small muscles situated in the elbow and for which no homologues can be found in a generalized labium. The secondary flexors run directly across the hinge line from the ventral wall of the postmentum to that of the prementum. The tertiary flexors originate on the postmentum distal to the secondary flexors and then run upwards to insert on the lateral walls of the proximal part of the prementum. Snodgrass (1954) believed that this last pair of muscles functions in maintaining tension on the folds that girdle the palpal adductors but it appears to me that they must be capable of performing some flexor function.

The hypopharynx (Fig. 13, 14 and 15) arises from the ventral wall of the head directly behind the mouth. It is cushion-like and narrowest at its base, and setae over its dorsal and lateral sides are directed towards the mouth. The hypopharynx is continuous with the postmentum through a wide membranous area and in this area the salivary duct opens into a pit (sal) whose sides contain sclerotized bars. These bars are continuations of the lateral walls of the hypopharynx, from which is also given off a large T-shaped apodeme (Tap) which runs into the base of the labium and is held there by three sets of ligaments. The apodeme in this form is characteristic of odonate larvae and is evidently associated with labial action. At the base of the T-shaped apodeme are inserted the retractors of the hypopharynx (rthyp) which, as Richard (1965) correctly pointed out, do not originate on the tentorium but on a shelf mesad of the labial base. The primary flexor muscles of the prementum (1° fl) arise one third of the way down the apodeme from the hypopharynx. The dorsal side of the apodeme is grooved and carries the salivary duct. The hypopharyngeal muscles of the mandible (vmh) arise on the base of the hypopharynx, and on the dorsal side is the suspensorium (susp), a transverse bar which is extended into two dorsal bars which pass up around the mouth.

Libellula quadrimaculata

The head capsule (Fig. 16 and 17) differs from that of *Aeshna interrupta* in several important respects. It is more hypognathous and not as flattened, and the labial palps are developed to such an extent that they cover the whole of the lower and front parts of the head when the labium is at rest. Associated with this is a peculiar development of the eyes that has been described by Lew (1933); only the dorso-lateral part of the eye is functional, the lower part that is covered by the labial palps remaining rudimentary and unpigmented until metamorphosis, when it forms most of the adult eye. The differences between *Aeshna* and *Libellula* in respect of the functional morphology of the larval eyes is considered by Pritchard (1966).

The shape of the face is such that there is a close association with the labial palps. A groove between the frons (fr) and the clypeus (cl) takes the distal edges of the labial palps, and the clypeus, labrum (lr), mandibles (ma), maxillae, and hypopharynx are normally hidden (Fig. 2). The frons (fr) bulges out above the labial palps and its dorsal border is marked by the attachments of the labral muscles internally. The rudiments of three ocelli can be seen on the vertex (vx), and the coronal (cs) and post-frontal (pfs) sulci are well defined. The antennae are probably more important in prey detection than those of *Aeshna*.

The posterior wall of the head capsule is not as concave as that of *Aeshna interrupta*, but is similar in all other respects. The posterior articulation of the mandible (pam) is supported by ridges associated with the occipital sulcus and the hypostoma. The external pits of the posterior (tp) and anterior (ta) arms of the tentorium are disposed in the bases of the post-occipital suture (pos) and just above the anterior articulations of the mandibles respectively. The tentorium (aat, pat) is *pi*-shaped and similar in all respects to that of *Aeshna interrupta*.

Apart from the labium, the essential features of the mouthparts of *Libellula quadrimaculata*

(Figs. 18-24) are similar to those of *Aeshna interrupta*. The dorsal muscles of the mandible are very large and the ventral muscles are small; the maxilla has a sharp-toothed lacinia and lacks a galea; the hypopharyngeal apodeme is well developed as a T-shaped rod.

In the labium (Fig. 23 and 24), the postmentum (pom) is relatively small but the prementum (prm) is large and widens considerably at its distal end. The palps are approximately triangular in shape and meet along the length of their inner edges at rest. In this position they form the front and sides of a cup-like arrangement with the prementum. The movable hooks (mh) are small and prey is usually caught between the inner edges of the palps. Long palpal and premental setae form a cage-like roof to the cup-shaped labium when it is extended (Fig. 25) and this structure undoubtedly aids in the retention of small, elusive prey such as cladocerans, ostracods and gammarids, which figure more prominently in the diet of libellulids than in aeshnids (Pritchard, 1964).

The muscles of the labium are the same as those in *Aeshna*, although the palpal adductors (addlp) and abductors (ablp) are especially large. The tentorial extensors of the prementum (exprm) insert through thin apodemes on lever-like extensions of the prementum past the hinge line. The primary flexors (1° fl) of the prementum originate at the anterior end of the T-shaped apodeme and insert on the latero-ventral walls of the proximal end of the prementum. The secondary flexors (2° fl) run from their origins on the ventral wall of the distal postmentum across the hinge line to insert on a lateral ridge on the prementum. The tertiary flexors (3° fl) have their origins distad of the secondary flexors on the postmentum, and they insert on the lateral walls of the prementum as in *Aeshna interrupta*.

LABIAL EXTENSION

It is clear that the T-shaped apodeme is involved in labial extension, either as support for the labial base or more actively as a structure on which muscles can pull, or perhaps in both capacities. Since the labium does not articulate with the head through sclerotized points, the T-shaped apodeme does indeed give some rigidity to the base of the labium. On the morphologically dorsal side of the labial base the postmentum is sclerotized only along a narrow band (Fig. 24), there being an area of unsclerotized cuticle proximally which allows the postmentum to swing forward on the head. The hypopharyngeal end of the apodeme is a fairly rigid point, being sclerotized and probably held in position by contraction of the retractor muscles of the hypopharynx. The cross-piece of the apodeme is firmly attached to the proximal end of the sclerotized portion of the ventral side of the postmentum (Fig. 24); proximal to this, the cuticle is not sclerotized. In this way the labial base is supported and when the postmentum swings forward on the head it can do so only in a fairly restricted plane. The T-shaped apodeme bends under pressure, thereby providing the hinge for the postmentum. This can be shown in a dissected specimen by holding the head and moving the postmentum forwards. Furthermore, under these conditions the apodeme, and thereby the postmentum, returns to its original conformation when the postmentum is released.

The primary flexor muscle of the prementum is attached to the T-shaped apodeme. It is inserted towards the anterior end and never more than one-third of the length of the apodeme from the hypopharynx (Fig. 15, 20, 24, 26). It is clear, therefore, that it cannot move the apodeme in the manner suggested by Richard (1965).

Pritchard (1965a) recorded the speed of labial protraction in several Anisoptera, and a summary of these data is provided in Table 1 together with recordings made by Richard (1970), Caillère (1972), and some further recordings made by the present author. The faster camera speeds used in this latest sequence have allowed a more detailed examination of the strike such as is presented in Figure 27, which shows a typical labial extension in *Aeshna canadensis*.

The palps start to open, followed some 40 msec later by gradual forward movement of the postmentum (Phase I) over about 30 msec. The postmentum moves slightly ahead of the prementum as the rate of forward extension increases (Phase II) over a further 20 msec. There follows very rapid protraction (20 msec) of the whole labium (Phase III), and it is this phase which is recorded in Table 1. The labium is held extended (Phase IV) for a period of about 40 msec, and then slowly retracts (Phase V) over about 140 msec with the prementum folding slightly ahead of the postmentum.

This is in marked contrast to the pattern seen in a dead specimen in which the labium is extended by sudden pressure on the sides of the thorax (Fig. 28). Here the palps do not open, the postmentum does not precede the prementum in the early stages, and the rate of forward movement actually decreases rather than increases in the final stages.

The ability to produce extension of the labium (although not opening of the labial palps) in dead larvae by the above method is one point of evidence that supports the hydraulic mechanism advanced by Snodgrass (1954) and based on an idea by Amans (1881). Further support came from the observations on the strike by Pritchard (1965a) and Caillère (1972), while Olesen (1972) actually recorded pressure changes in the thorax during labial extension and correlated these with electrical activity in muscles on both sides of the abdominal diaphragm in a number of Anisoptera.

Olesen (1972) showed that pressure in the thorax of *Cordulia aenea* and *Sympetrum* sp. rises gradually over a period of about 200 msec, then increases rapidly over 20-30 msec, is held steady for about 70 msec, and then slowly falls over about 400 msec. It is not clear exactly when labial extension occurs, but the similarity between Olesen's graph of pressure changes and Figure 27 of the present paper strongly suggests that it occurs as a result of the strong contraction of the thoracic and abdominal muscles that produces the rapid pressure increase.

But extension of the labium is clearly not controlled solely by blood pressure. There are important differences between extension in living and dead specimens and, as Olesen (1972) has shown, the pressure waves that are responsible for jet propulsion are produced by the same muscles that are involved in labial extension. The fact that the labium is not extended during jet propulsion suggests some sort of locking mechanism. It would appear that this locking mechanism is to be found, in part at least, in the muscles attached to the T-shaped apodeme.

Consideration of the morphology of the labium, observations on the strike, and the recordings of pressure changes allows the construction of an hypothetical scheme of events that occur during labial extension. This scheme is arbitrarily divided into five phases, some of which are further divided. Reference to Figures 24 and 27 should aid in following the description of these events.

- Phase I. a) Abductor muscles of the labial palps contract and open the palps;
 b) Retractor muscles of the hypopharynx and primary flexors of the prementum contract and hold the hinge of the labium firm;
 c) Lateral muscles of the thorax and abdomen contract, and pressure builds up in the body cavity forcing the postmentum to swing forward slightly;
 d) Extensor muscles of the prementum probably contract but their action is counteracted by the combined action of the flexors.
- Phase II. a) Anus closes;
 b) Thoracic and abdominal muscles contract rapidly and the pressure wave is directed forwards into the labium so that

- the postmentum swings forward more rapidly.
- Phase III. a) Flexor muscles of the prementum suddenly relax allowing the extensor muscles to extend the prementum and combine with the pressure surging into the labium to rapidly protract the whole structure. The base of the T-shaped apodeme bends thereby providing the hinge on which the postmentum swings;
- b) The adductors of the labial palps contract, closing the palps.
- Phase IV. The pressure is maintained, holding the labium in the extended position.
- Phase V. a) The three pairs of flexor muscles of the prementum fold the prementum on the postmentum.
- b) The abdominal and thoracic muscles relax, the pressure decreases, and the postmentum returns to its resting position through the elastic properties of the T-shaped apodeme.

Thereafter slight pressure can be maintained at the labial base and can combine with the flexors and extensors of the prementum and the adductors and abductors of the palps to manipulate captured prey.

No cuticular catch mechanism is envisaged such as is found in mantid shrimps (Burrows, 1969), but then the strike in dragonfly larvae is very much slower. Although the action of the premental flexors in opposing extension of the prementum is likely to be rather weak, it is probably sufficient to explain the differences in movement and timing between normal and induced strikes. Unfortunately the small size of the dragonfly labium makes the replacement of the normal forces with known and controllable forces difficult, and the involvement of hydraulic forces adds further problems to any attempt at simulating the system.

This hypothesis does appear to successfully account for the following observations: Olesen's (1972) recordings of pressure changes; Caillère's (1972) observations on labial extension in *Agrion splendens* Harris in which the labium moves slowly forwards well before the actual strike and then is released rapidly; present observations on the phases of the strike of *Aeshna canadensis* summarized in Figure 27; the labium is not protracted during the early phases of pressure build-up nor during jet propulsion; the extension of the labium is more rapid in living animals than in dead ones, and in particular the phase of very rapid extension of the prementum does not occur in dead specimens; the postmentum returns to its resting position without the benefit of muscle action.

Table 1. The speed of the strike in various species of Odonata.

Species	Camera speed (fps)	No. of film frames	Time for major forward thrust of labium (msec)	Author
<i>Aeshna eremita</i> Scudder	64	1-2	15-30	Pritchard (1965)
<i>Cordulia shurtleffi</i> Scudder	64	1	15	"
<i>Leucorrhinia hudsonica</i> Selys	64	1	15*	"
<i>Anax</i> sp. and <i>Aeshna</i> sp.	64	1-2	20	Richard (1970)
<i>Agrion splendens</i> Harris	64	2	30	Caillère (1972)
<i>Aeshna canadensis</i> Walker	200	3-4	15-20	Present work
<i>Argia vivida</i> Hagen	200	2	10	"

* includes opening of the labial palps

THE ACTION OF THE OTHER MOUTHPARTS

Retraction of the labium brings the prey back to the other mouthparts where the mandibles are in a position to cut it up. The mandibles are powerful and heavily sclerotized and their movement is one of strong adduction and weaker abduction in a single plane. The mandibular articulations with the head capsule are well supported and allow the tips of the mandibles to move only in a plane at right angles to the longitudinal axis of the body, and as one mandible passes over the other the food is crushed and sliced.

If the food is soft the laciniae play no part in breaking it up, but they pass the chewed food back over the hypopharynx to the mouth. The spines and stiff setae on the lacinia are well designed for taking both large and small pieces of food which drop from the mandibles, and passing them back to the mouth. The movement of the maxillae is rather complex since there are vertical as well as horizontal components; basically, however, their movement is one of protraction and retraction in the horizontal-longitudinal plane, with a transverse-horizontal component introduced by the actions of the adductors of the cardo and stipes. The tip of the maxilla thus traces a roughly oval path. The forward movement is largely produced by the rotator of the maxilla and the adductor of the cardo, but the retraction is stronger and involves the adductor of the stipes and the cranial flexor of the lacinia. The stipital flexor of the lacinia adds to the further flexing of the lacinia on the stipes. Elasticity of the cuticle is important in certain components of the outward movement of the maxilla, particularly in the extensions of the lacinia and the stipes.

When the prey is easily chewed by the mandibles, these and the maxillae work alternately at a steady rate; as the mandibles open and release the chewed pieces of food, the laciniae move inwards and backwards taking the food with them. The rate of chewing depends on many factors including the size of the prey and its activity, and the manner in which it is being held by the labial palps. The average rate for eleven *Aeshna interrupta lineata* larvae, 22 to 29 mm in length, eating *Aedes aegypti* larvae at 15° C in the laboratory, was 54 cycles per minute.

If the prey is hard the regular activity of the mandibles and maxillae is modified. The action of the maxillae becomes more complex and their cycles of protraction and retraction do not necessarily keep in phase with the action of the mandibles. The movements of the mandibles are irregular, depending on whether they are successful in breaking up the cuticle of the prey, and the spines of the lacinia are also used from the start to help to tear the food apart. When working on hard parts, the laciniae pass food back at irregular intervals, but when soft parts are exposed there is a return to the regular alternating actions of the mandibles and maxillae.

The labrum serves to prevent food from floating away and may also function in directing it towards the mandibles, for it is raised and moved forward slightly as the mandibles open and then is drawn back as the mandibles close. The ventral side of the labrum is the site of gustatory sensilla (Pritchard, 1965b).

Food that is passed back by the maxillae is directed towards the mouth by setae on the dorsal side of the hypopharynx. The hypopharynx is probably also the site of sensilla.

During feeding the prey is manipulated by the labium, the mandibles and the maxillae. The labium is held so that the food is in the correct position for the mandibles to work on it. This usually demands that the postmentum is swung forward and presumably controlled blood pressure plays a role here. The prey is often taken between the two mandibles while the labial palps change their grip. Occasionally the prey is lost and floats upwards and then another strike will often be made, but pieces of food that drop from the mouthparts are not usually recovered.

The spatulate prementum of aeshnids acts as a plate which collects many particles that fall from the mandibles and maxillae, and these pieces are retrieved by the maxillae at the end of the meal. The cup-like labium of the libellulids is even more efficient in collecting these food

particles, and the arrangement of palpal and premental setae prevents the escape of food upwards.

At the end of the meal the mouthparts are cleaned, particularly the labial palps, which are opened and closed several times to remove all traces of the last meal. The front legs may also be used to clean the labium.

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ACKNOWLEDGEMENTS

Most of the morphological work reported in this paper was included in a thesis submitted to the University of Alberta, and I am grateful to the many people who provided advice, encouragement and facilities at that time. I also thank Dr. D. A. Craig for comments on the manuscript.

LIST OF ABBREVIATIONS USED IN FIGURES

1° fl	primary flexor of prementum	mh	movable hook of labial palp
2° fl	secondary flexor of prementum	mlra	anterior labral muscle
3° fl	tertiary flexor of prementum	mlrp	posterior labral muscle
aat	anterior arm of tentorium	mo	molar ridge of mandible
ablp	abductor of labial palp	mxp	maxillary palp
adcd	adductor of cardo	o	occiput
addlp	adductor of labial palp	oc	ocellus
adst	adductor of stipes	os	occipital sulcus
bz	budding zone of compound eye	pam	posterior articulation of mandible
cd	cardo	pat	posterior arm of tentorium
ce	compound eye	ped	pedicel
cl	clypeus	pfs	postfrontal sulcus
cplr	compressor of labrum	pg	postgena
cs	coronal sulcus	po	postocciput
dab	dorsal abductor of mandible	pom	postmentum
dad	dorsal adductor of mandible	pos	postoccipital suture
dat	dorsal arm of tentorium	prm	prementum
dpmp	depressor of maxillary palp	rthyp	retractor of hypopharynx
eh	end-hook of labial palp	rtmxa	rotator of maxilla
exprm	extensor of prementum	sal	salivarium
flec	cranial flexor of lacinia	sc	scape
flcs	stipital flexor of lacinia	sens	location of gustatory sensilla
for	occipital foramen	stp	stipes
fr	frons	susp	suspensorium of hypopharynx
gen	gena	ta	anterior tentorial pit
in	incisor area of mandible	Tap	apodeme of hypopharynx
hyp	hypopharynx	td	dorsal tentorial macula
lb	labium	tp	posterior tentorial pit
lc	lacinia	vmh	ventral hypopharyngeal muscle of mandible
lp	labial palp	vmt	ventral tentorial muscle of mandible
lr	labrum	vx	vertex
lvmp	levator of maxillary palp		
ma	mandible		
max	maxilla		

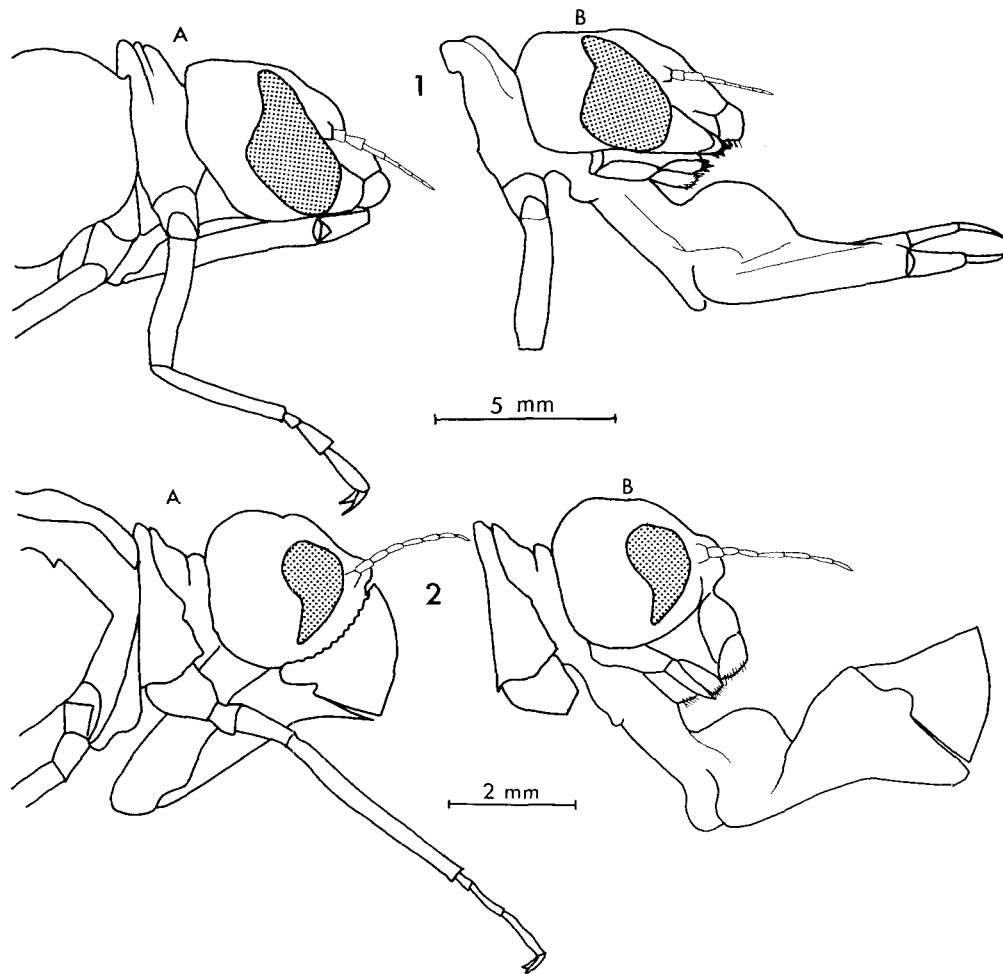


Fig. 1. Lateral view of the head of a last instar larva of *Aeshna interrupta lineata* Walker with the labium A) retracted and B) extended. Fig. 2. As Fig. 1 but for *Sympetrum danae* Sulzer.

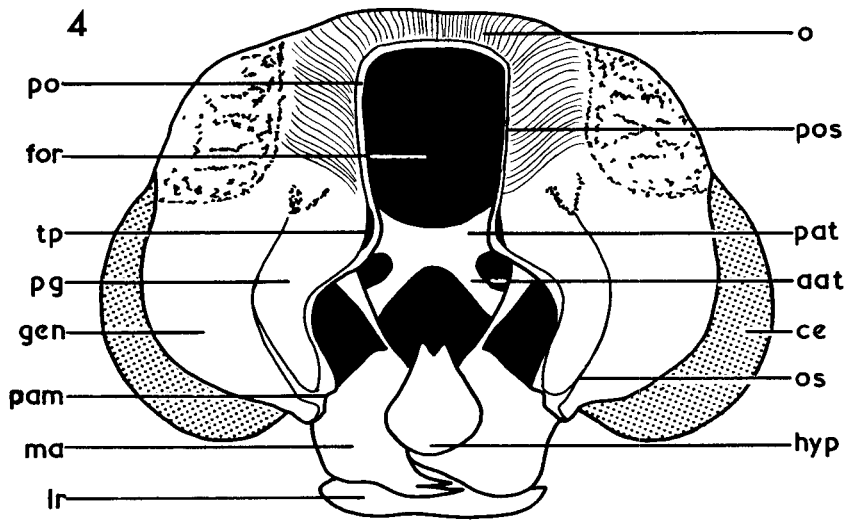
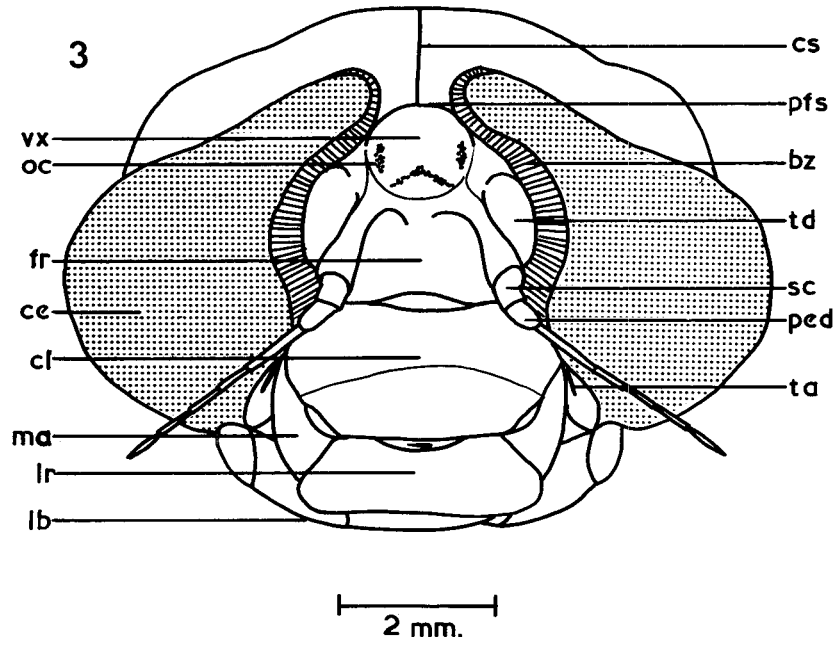


Fig. 3. Anterior view of the head capsule of a last instar larva of *Aeshna interrupta lineata*. Fig. 4. As Fig. 3 but posterior view.

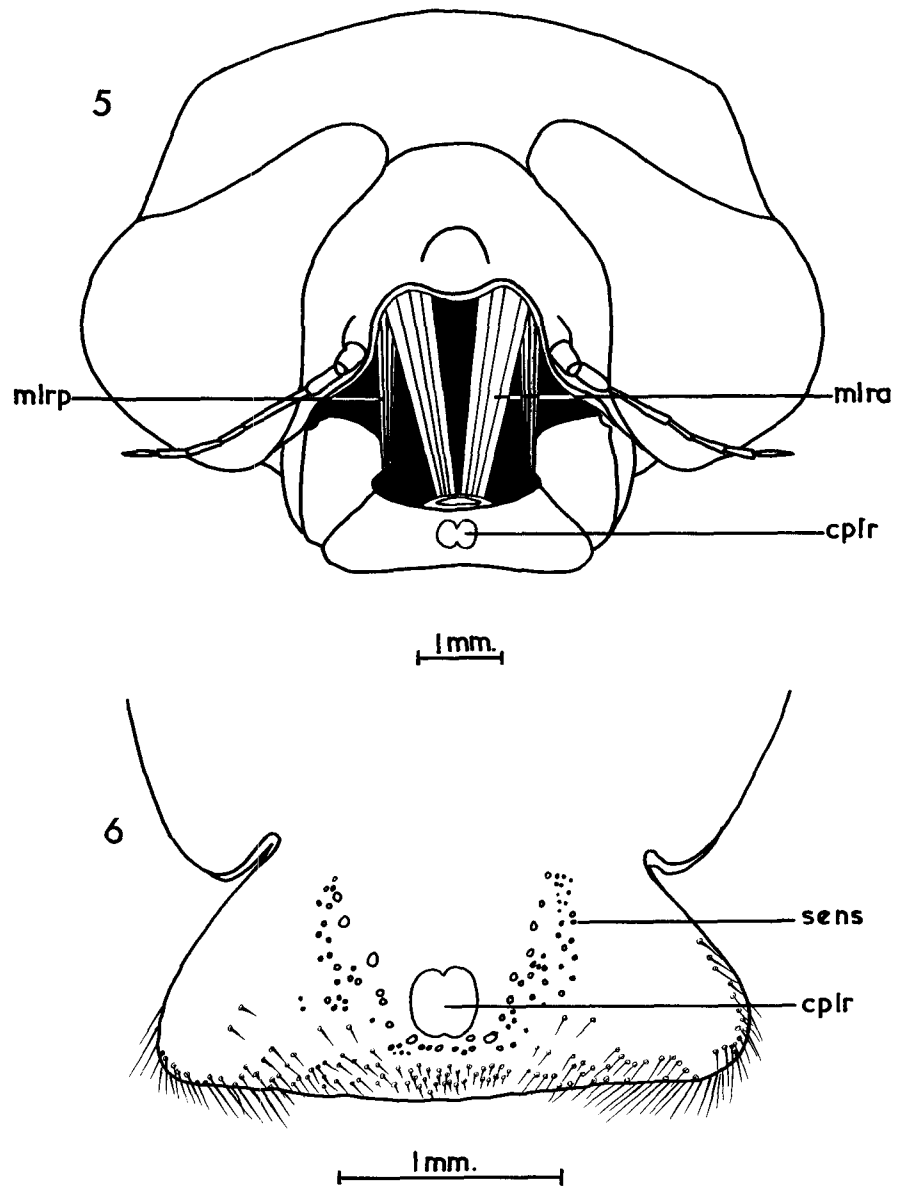


Fig. 5. Anterior view of the head of *Aeshna interrupta lineata* dissected to show the labral muscles. Fig. 6. Ventral view of the labrum of *Aeshna interrupta lineata*.

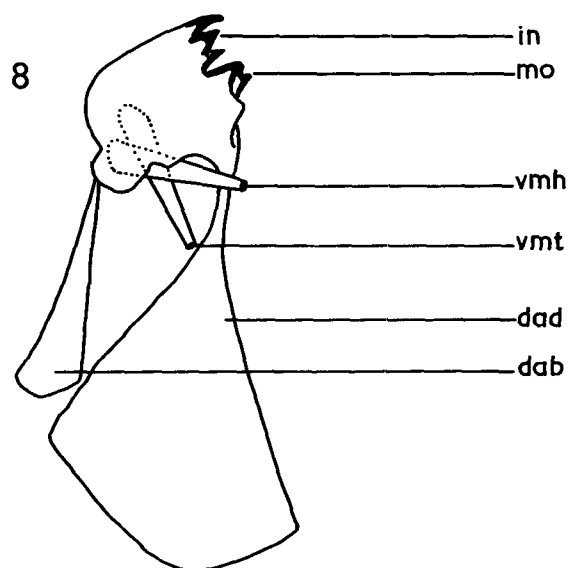
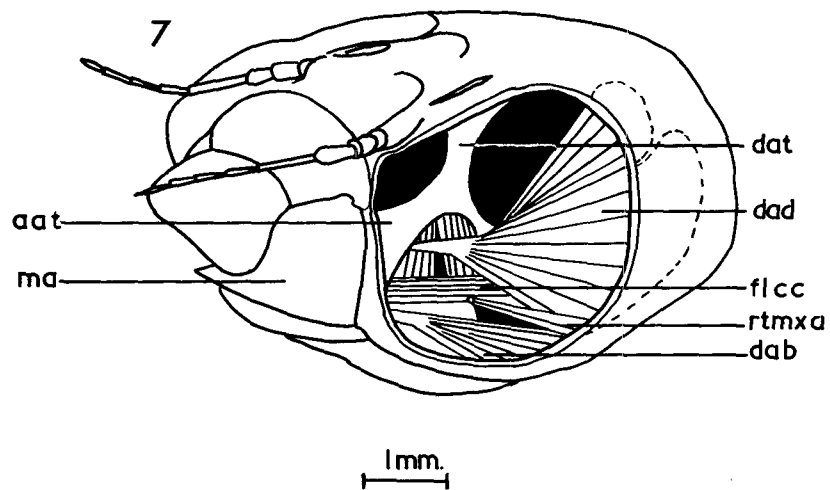


Fig. 7. Lateral view of the head of *Aeshna interrupta lineata* dissected to show the dorsal mandibular muscles and some maxillary muscles. Fig. 8. Anterior view of the left mandible of *Aeshna interrupta lineata*.

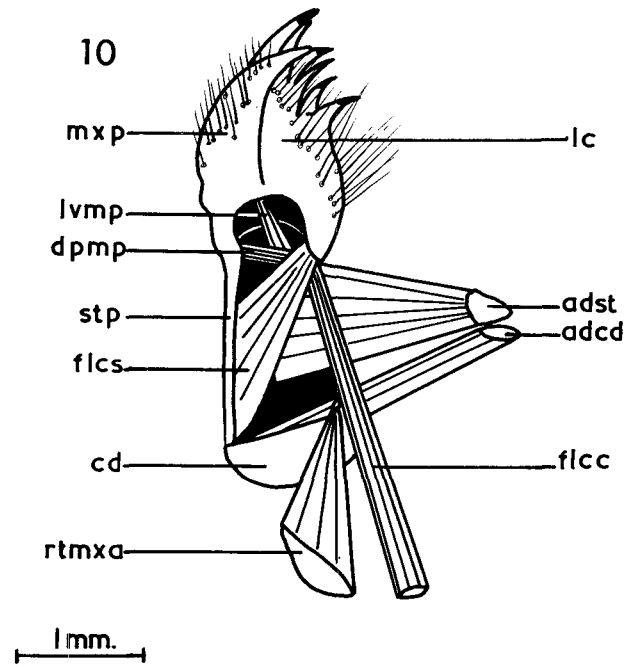
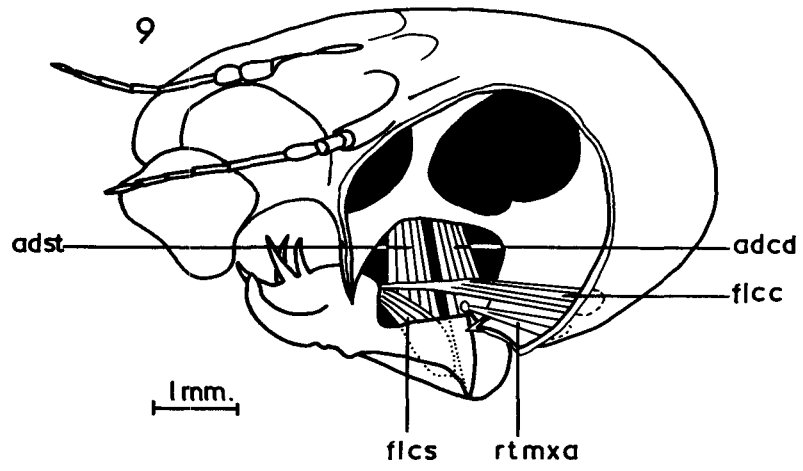


Fig. 9. Lateral view of the head of *Aeshna interrupta lineata* dissected to show the maxillary muscles. Fig. 10. Anterior view of the left maxilla of *Aeshna interrupta lineata*.

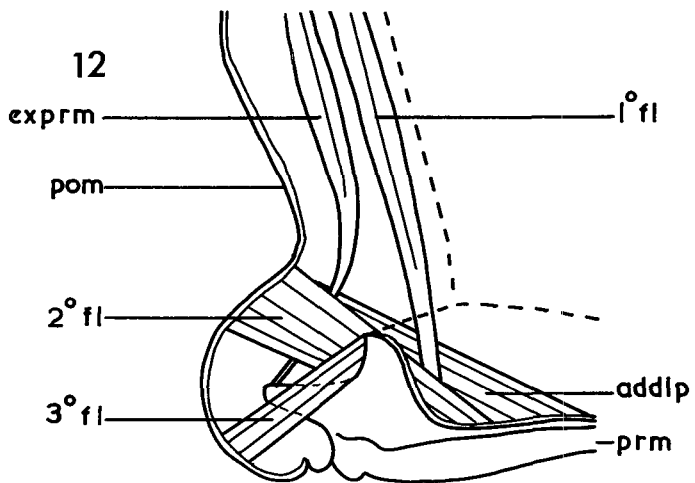
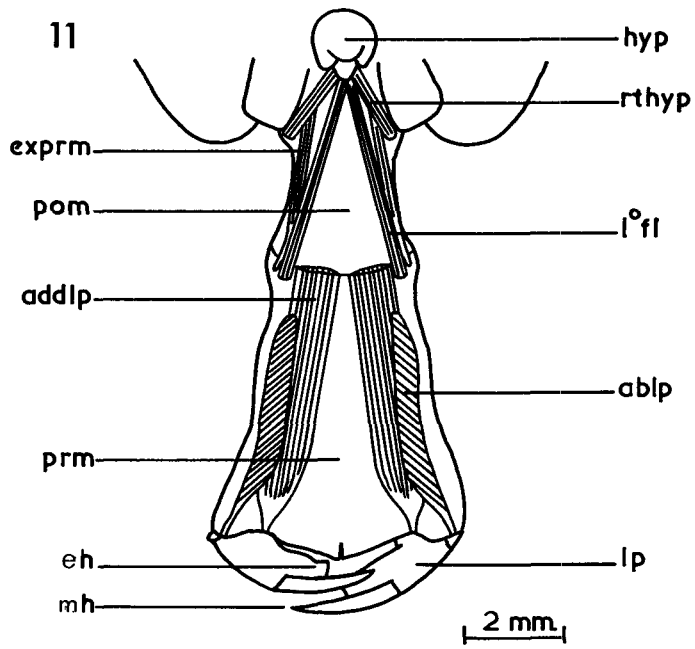


Fig. 11. Dorsal view of the labium of *Aeshna interrupta lineata* dissected to show the muscles. Fig. 12. Lateral view of the elbow muscles in the labium of *Aeshna interrupta lineata*.

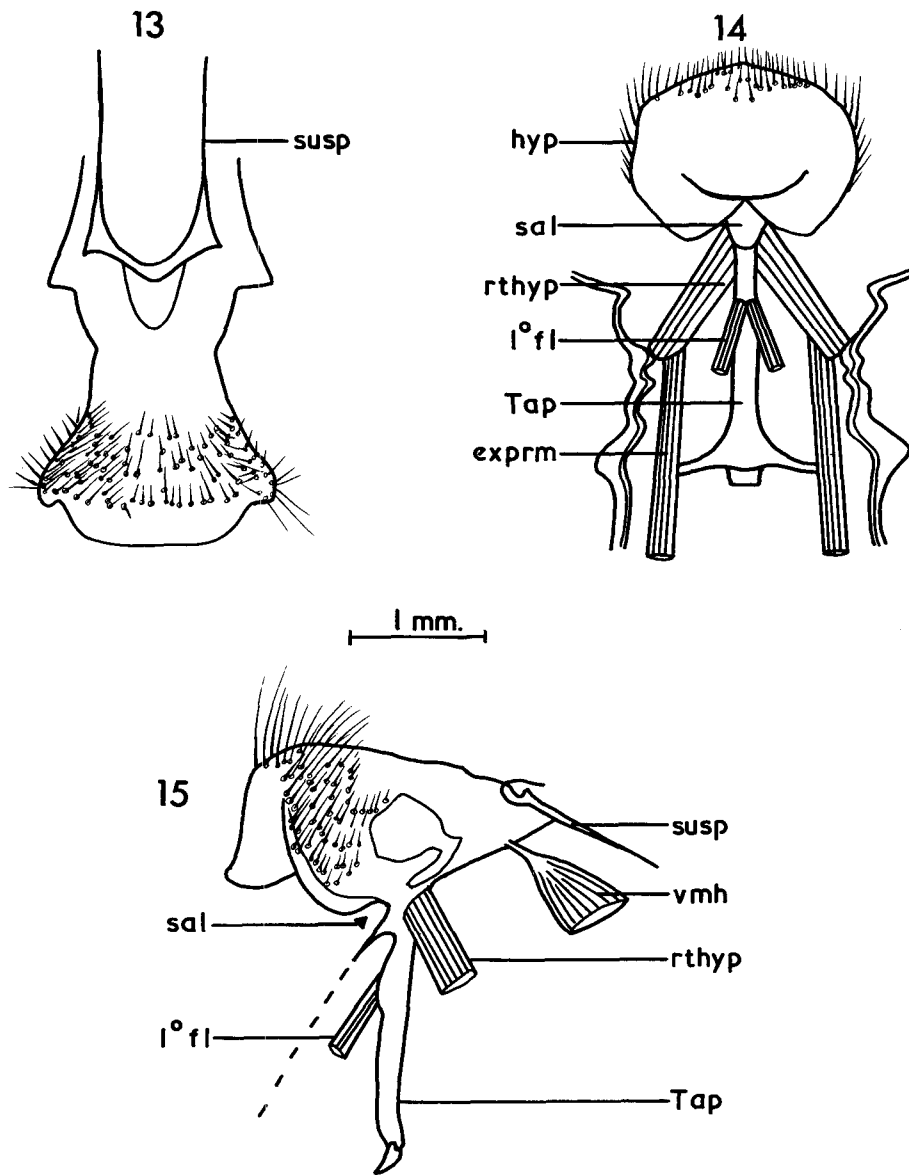


Fig. 13. Anterior view of the hypopharynx of *Aeshna interrupta lineata*. Fig. 14. Ventral view of the hypopharynx of *Aeshna interrupta lineata* dissected to show the muscles. Fig. 15. Lateral view of the hypopharynx and associated muscles in the labial base of *Aeshna interrupta lineata*.

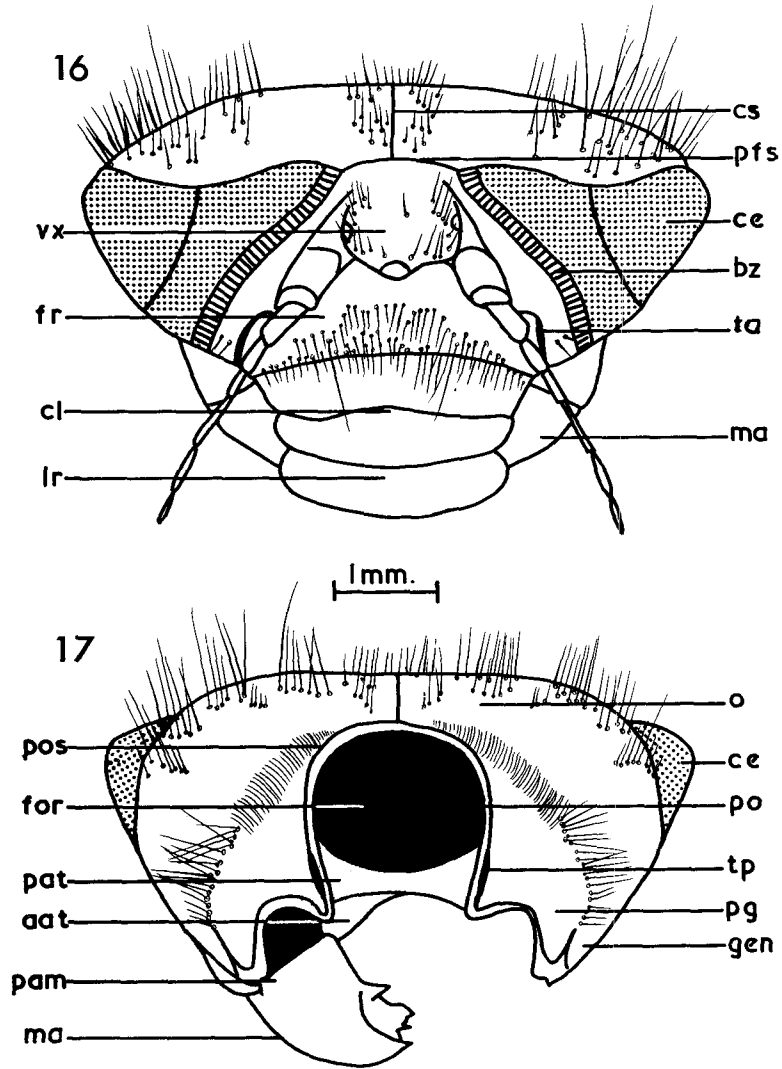


Fig. 16. Anterior view of the head capsule of a last instar larva of *Libellula quadrimaculata* L. Fig. 17. As Fig. 16 but posterior view.

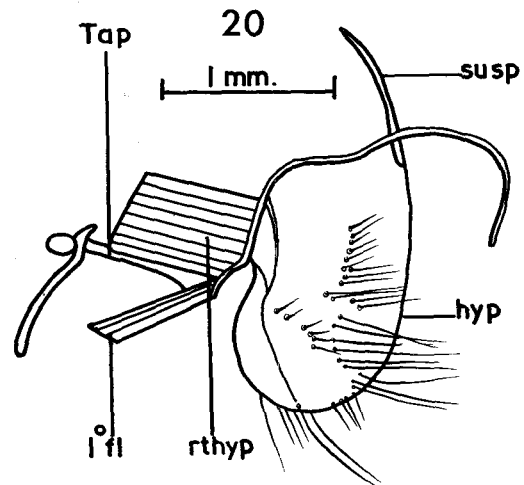
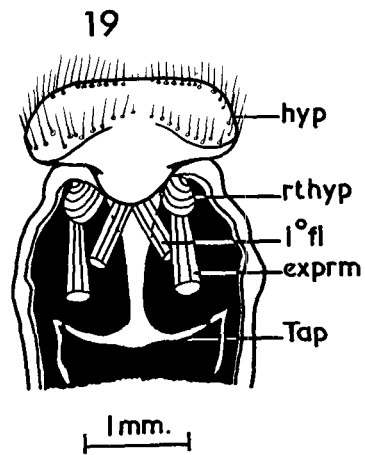
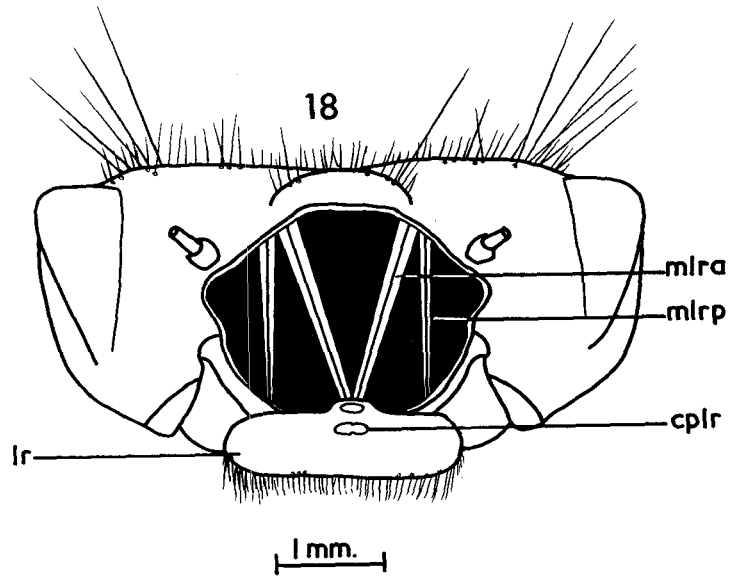


Fig. 18. Anterior view of the head of *Libellula quadrimaculata* dissected to show the labral muscles. Fig. 19. Ventral view of the hypopharynx of *Libellula quadrimaculata* with the labial base dissected to show the muscles. Fig. 20. As. Fig. 19 but lateral view.

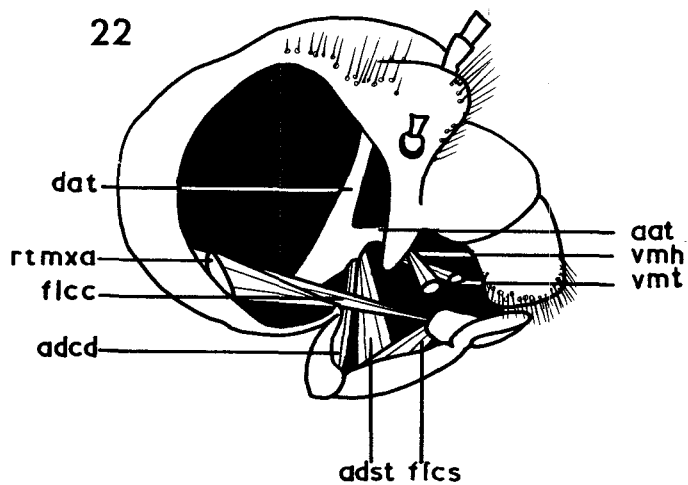
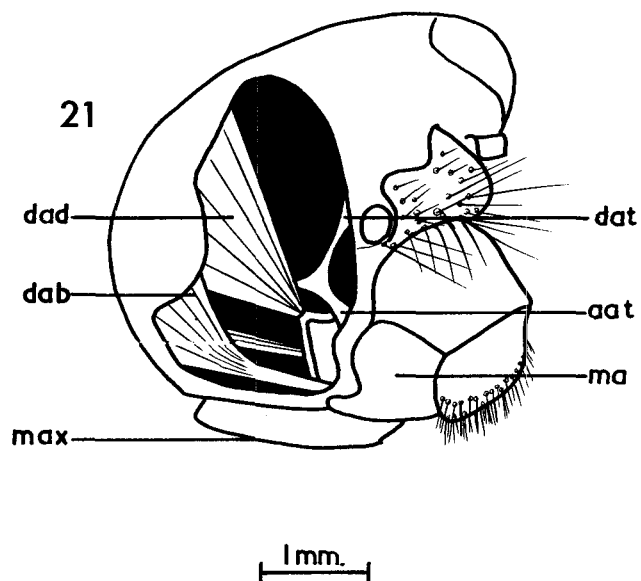


Fig. 21. Lateral view of the head of *Libellula quadrimaculata* dissected to show the dorsal mandibular muscles. Fig. 22. As Fig. 21. but showing the maxillary muscles and ventral mandibular muscles.

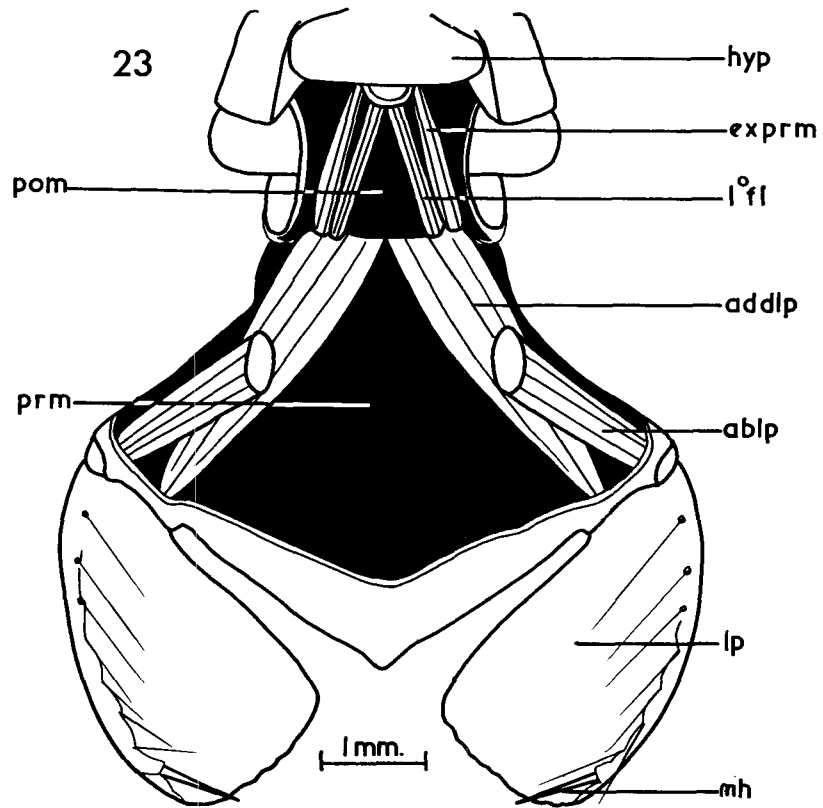


Fig. 23. Dorsal view of the labium of *Libellula quadrimaculata* dissected to show the muscles.

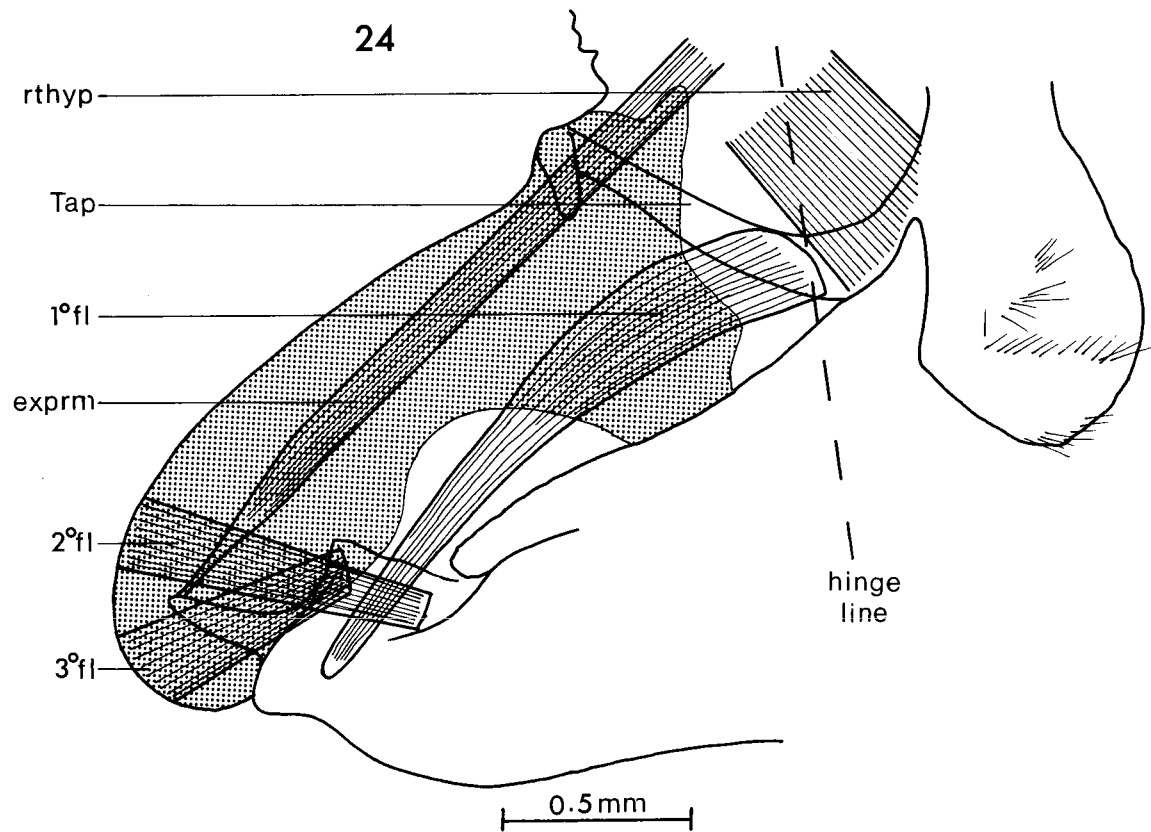


Fig. 24. Lateral view of the labium and hypopharynx of *Libellula quadrimaculata* showing the muscles and with stippling to show the extent of sclerotization in the postmentum.

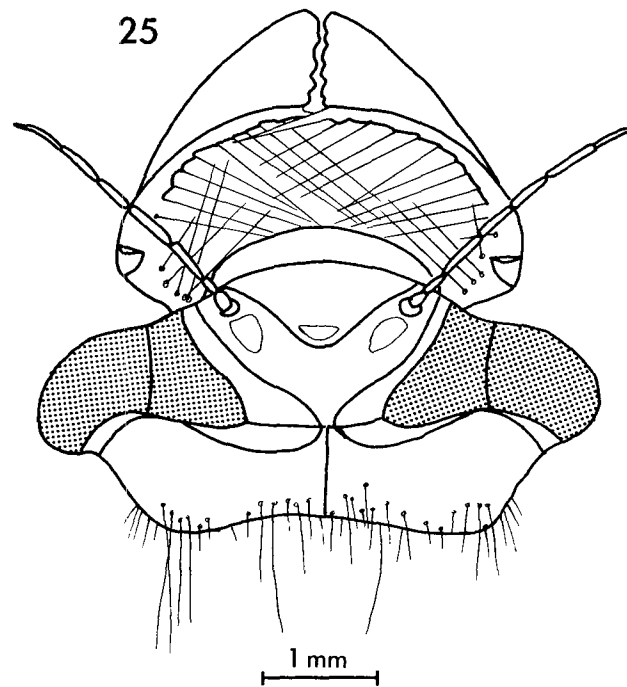


Fig. 25. Dorsal view of the head of *Leucorrhinia intacta* with labium partly extended to show the cage-like roof formed by palpal setae.

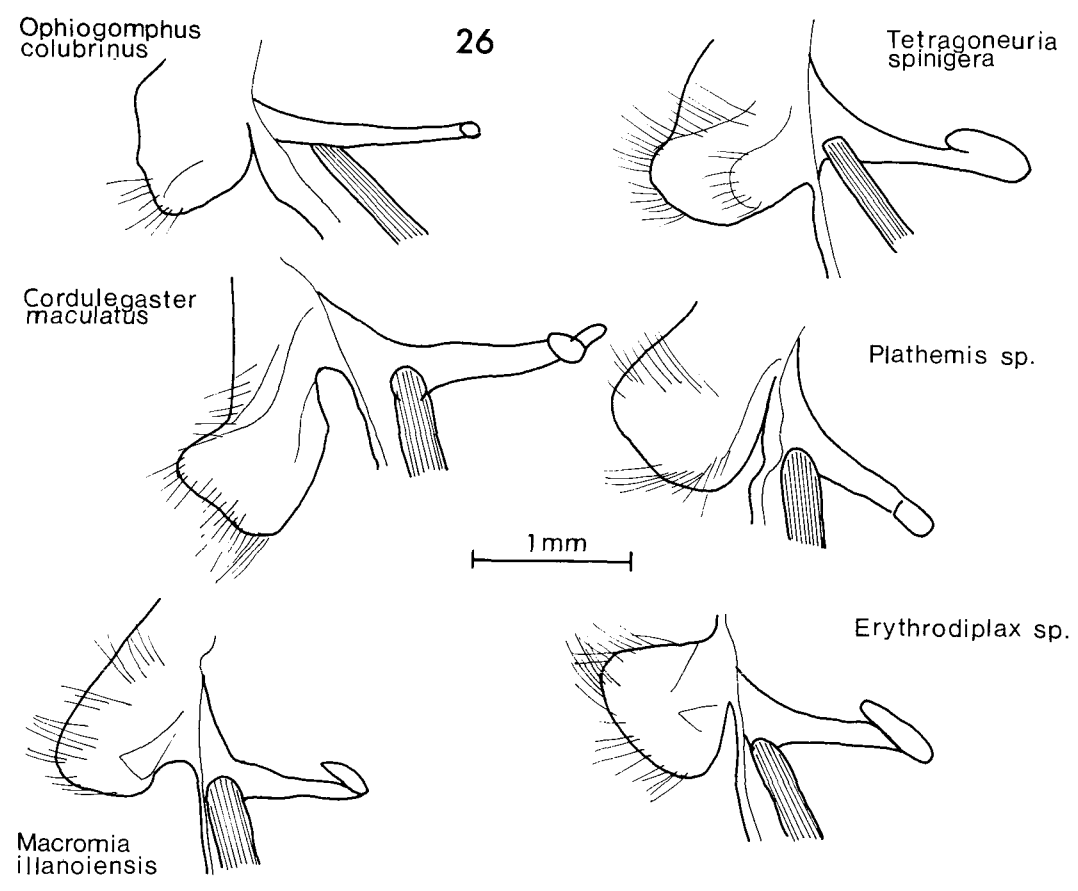


Fig. 26. The hypopharyngeal apodeme and attachment of the primary flexor of the prementum in six species of Anisoptera.

27

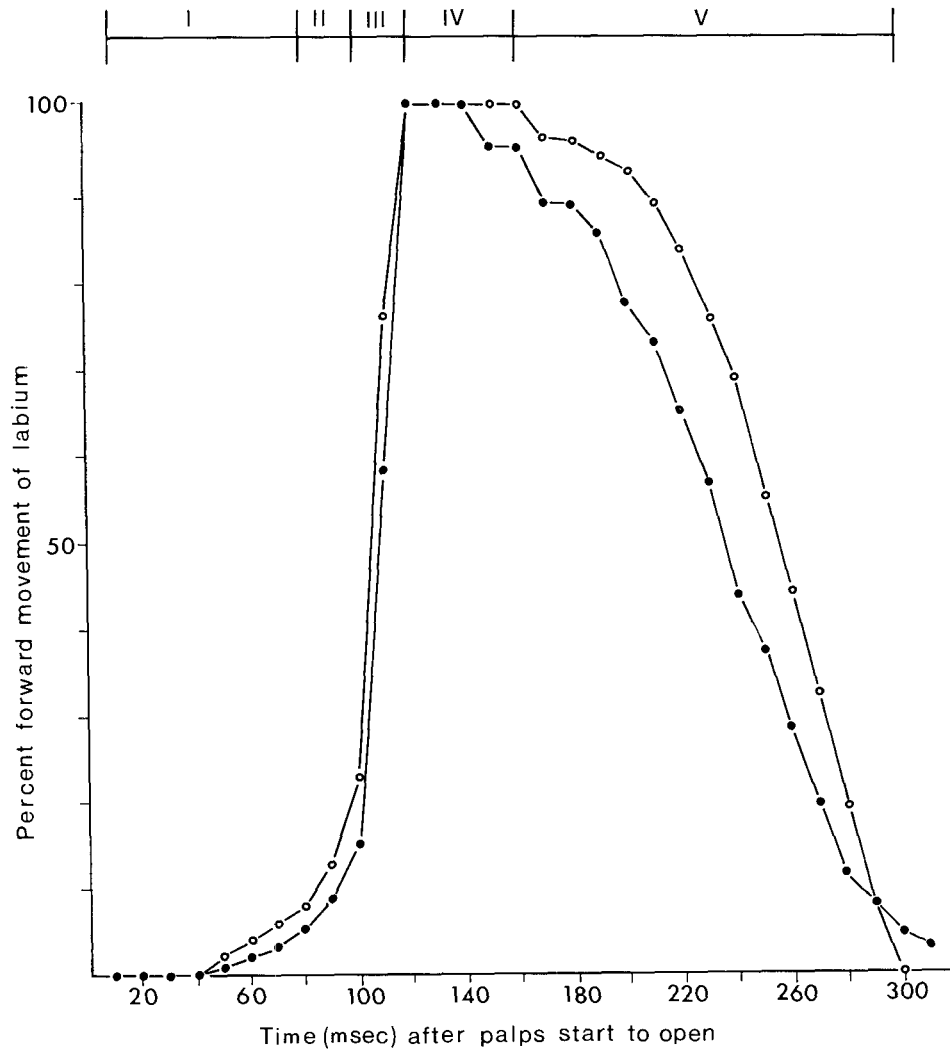


Fig. 27. Forward movement of the distal postmentum (open circles) and distal prementum (closed circles) during a typical strike by an *Aeshna canadensis* larva. The phases of the strike referred to in the text are indicated by Roman numerals.

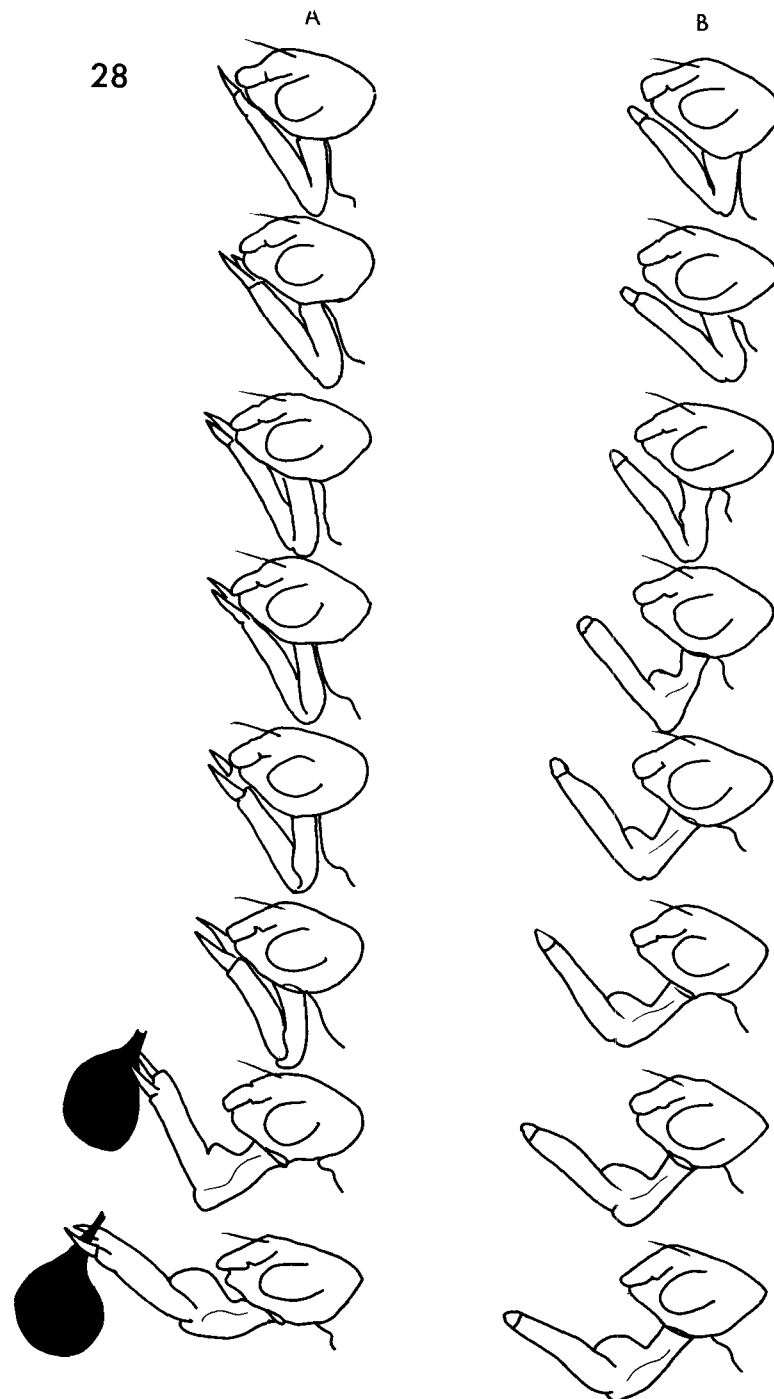


Fig. 28. Protraction of the labium in larvae of *Aeshna canadensis*. A) normal strike; B) extension produced by sudden pressure on the thorax of a recently killed larva. The interval between stages is 10 msec.